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Biostratigraphy of the Casamayoran, Early Eocene, of Patagonia

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ABSTRACT

The Casamayoran, presumed to pertain to the early Eocene, is the most diverse and best known of South America's early to middle Tertiary land mammal ages. Because the composition of local faunas and the stratigraphic position of assemblages at any given locality have not been evaluated, however, the Casamyoran has remained a dimensionless age, despite its seminal importance to understanding the early radiations of mammals on the South American continent.

Preliminary analysis of field data and collections obtained by G. G. Simpson in 1930–1931 suggests a faunal succession in the Casamayoran of Patagonia. Large, well documented samples are available from two localities with relatively wide stratigraphic distributions of Casamayoran mammals: Cañadón Vaca and the Gran Barranca south of Lago Colhué Huapí, central Chubut. The compositions of these two local faunas differ markedly, and lithostratigraphic, biostratigraphic, and paleontologic evidence suggests that these differences are temporal and not ecological in nature. Faunal composition of the two localities is compared qualitatively and statistically with respect to the magnitude of difference seen in preceding and succeeding South American land mammal ages and to roughly equivalent North American land mammal ages. Two new subdivisions of the Casamayoran, the Barrancan and the Vacan, are defined on this basis. In addition, a composite stratigraphic plot of taxa from the younger of the two localities (the Gran Barranca) produced a number of non-overlapping range zones within the Barrancan; statistical analysis indicates that the probability these observations are due to sampling error is small in most, but not all, cases. The other Patagonian local faunas are briefly considered with respect to this scheme, and an hypothesis of their relative ages is presented.

INTRODUCTION

It is now widely accepted that South America was an island continent for most of the Tertiary—insular, or nearly so, with respect to its biota. The Tertiary record of South

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America's mammalian faunas is fairly well known and, as a consequence, provides an ideal "natural experiment" for the study of historical biogeography and evolutionary principles in general. Of particular interest are the earliest faunas, those from the beginning of the Age of Mammals, because they are critical to understanding the phylogeny, adaptive radiations, and biogeographic deployment of mammals on the South American continent. Of these early assemblages, the Casamayoran is by far the most diverse and well known.

The great Argentine paleontologist, Florentino Ameghino, who first described the "*Notostylops*" (Casamayoran) fauna, believed it to include dinosaurs and thus considered it to be Late Cretaceous in age. This view has long since been shown to be incorrect (Simpson, 1932) but, because the mammalian fauna is so dissimilar to those from anywhere else in the world, the age of the Casamayoran is not well established in either relative or radiometric terms. Simpson (1940) considered the age of Patagonian marine formations and placed the Casamayoran in the early Eocene.[2] Welcome new evidence, in the form of radiometric dates and a magnetic polarity sequence, is now at hand for part of the underlying Río Chico Formation, fixing its age as 61 to 56 million years (Marshall et al., 1981). Such data are not yet available for rocks enclosing a Casamayoran fauna and the Riochican-Casamayoran boundary is placed, by convention, at the Paleocene boundary (Marshall, 1982).

Despite nearly a century of effort, South America's early land mammal history is so inadequately documented that only very general observations can be made. A critical missing element is a precise chronology, either absolute or relative. The stratigraphic relationships of the faunas have not yet been evaluated and, because little attention has been paid to variation between the composition of local faunas or to the superposition of assemblages from given localities, the Casamayoran has remained an age without temporal dimension.

The collections made in central Patagonia by the Scarritt Patagonian Expeditions (1930–1931, 1933–1934), under the direction of George Gaylord Simpson, are of paramount importance in this regard. Today, more than 50 years later, they include the largest collections of Casamayoran mammals and are the only ones for which precise stratigraphic provenience data are available. In the present paper I present the stratigraphic data for large, well documented samples from two localities with relatively wide stratigraphic distributions of Casamayoran mammals and consider the composition of other Patagonian local faunas of Casamayoran age.

[2] By suggesting that the arctostylopid *Palaeostylops*, of the Gashato fauna, Mongolia, was Paleocene in age and ancestral to both the Wasatchian *Arctostylops* and the notoungulates of South America, Matthew and Granger (1925) had already implied that the earliest Nearctic forms (i.e., those of the Casamayor fauna; the Riochican was not then known) were of latest Paleocene or early Eocene age.

Acknowledgments

I am deeply grateful to the late Dr. George Gaylord Simpson for his advice and for permission to use his fieldnotes of the Scarritt Patagonian Expeditions. All original field observations and descriptions presented herein were made by him and are directly abstracted from these notes, now deposited in the archives of the Department of Vertebrate Paleontology, American Museum of Natural History. This paper is therefore largely the results of Simpson's efforts, although I of course assume full responsibility for any misinterpretations I may have introduced. I dedicate this paper to his memory. I thank Dr. Malcolm C. McKenna of the Department of Vertebrate Paleontology for access to the collections and notes of the Scarritt Expeditions. Helpful review comments on an earlier draft of this paper were provided by Drs. McKenna, L. G. Marshall, D. Savage, and R. H. Tedford, and their advice is warmly appreciated. Partial support for this research was provided by the Undergraduate-Graduate Research Program administered by the American Museum of Natural History and supported by the Greenwall Foundation.

HISTORICAL AND GEOLOGICAL BACKGROUND

The first mammals to be described from what is now known as the Casamayoran were

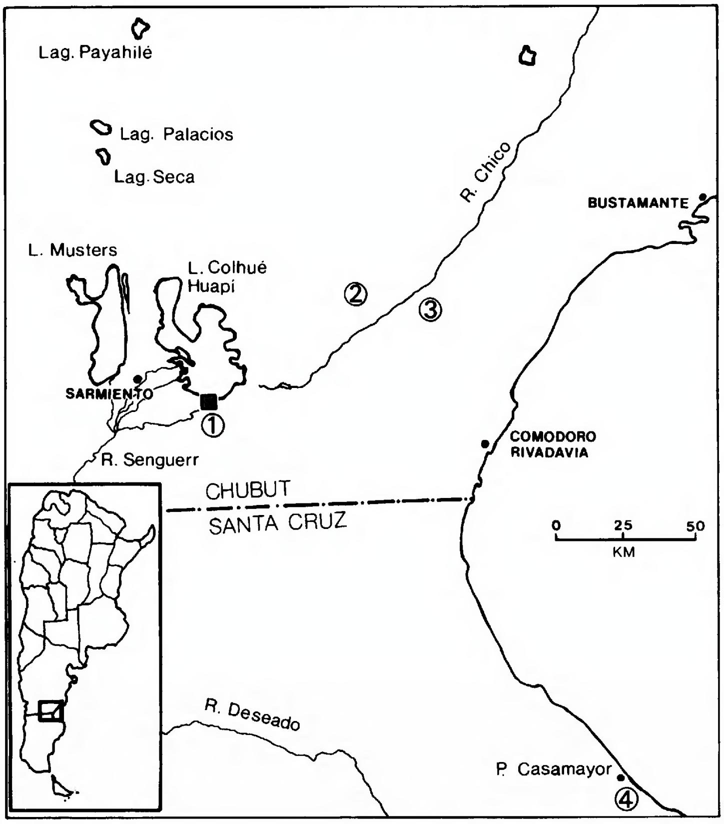

FIG. 1. Central Patagonia index map. Localities: 1, Gran Barranca south of Lago Colhué Huapí (black rectangular area; shown in greater detail on fig. 2); 2, Cañadón Vaca; 3, Cañadó Hondo; 4, Cañadón Lobo. Tapera de López, not on the map, is approximately 30 km northeast of Laguna Palacios; the exact location of several other (Ameghino) localities is uncertain.

collected by Carlos Ameghino at the Gran Barranca south of Lago Colhué Huapí, central Chubut, in 1895–1896, and were published by Florentino Ameghino (1897) in his second work devoted to the *Pyrotherium* (Deseadan) fauna. Carlos later noted (Ameghino, 1913–1936, vol. 21, p. 105) that the fossils in question pertained to a much earlier, pre-*Pyrotherium,* fauna and, following Carlos' suggestion, Florentino named this the *Notostylops* fauna after that characteristic and abundant genus (Ameghino, 1899). Florentino Ameghino subsequently (1902) distinguished two subdivisions of the *Notostylops* fauna and later (1903) added a "basal" part. In his great treatise of 1906, Ameghino abandoned these somewhat hypothetical subdivisions but noted that a large span of time was probably represented and that perhaps three or even four distinct faunas were included. The French collector Andre Tournouër, guided by Carlos Ameghino, made a small collection of Casamayoran mammals at Cañadón Lobo, near Punta Casamayor, and "Casamayoran" has since been adopted as the geographic term for Ameghino's *Notostylops* fauna (Simpson, 1933).

In addition to the Gran Barranca and Cañadón Lobo, a number of other localities in Patagonia have yielded Casamayoran mammals; these have been reviewed by Simpson (1948, 1967a) and Marshall et al. (1983). Some of the localities under consideration here are shown in figure 1; these and others for which data are available are included in the Casamayoran local fauna lists of table 1.

Mammalian fossils of Casamayoran age in

TABLE 1
Composition of Casamayoran Local Faunas[a]

Species	Localities[b]											
	1	2	3	4	5	6	7	8	9	10	11	12
Coona pattersoni Simpson, 1938	–	–	X	–	–	–	–	–	–	–	–	–
Coona gaudryi Simpson, 1964	X	–	–	–	–	–	–	–	–	–	–	–
Caroloameghinia mater Ameghino, 1901	X	–	–	–	–	–	–	–	–	–	–	–
C. tenuis Ameghino, 1901	–	–	–	–	–	–	–	–	–	–	–	X
Arminiheringia auceta Ameghino, 1902	?X	–	–	?X	–	–	–	–	–	–	–	–
Patene coluapiensis Simpson, 1935	X	–	–	–	–	–	–	–	–	–	–	–
Polydolops thomasi Ameghino, 1897	X	X	–	–	–	–	–	–	–	–	–	X
P. serra Ameghino, 1902	X	–	–	–	–	–	–	–	–	–	–	–
P. princeps (Ameghino, 1902)	X	–	–	–	–	–	–	–	–	–	–	–
P. primulus (Ameghino, 1902)	X	–	–	–	–	–	–	–	–	–	–	–
P. borcurhor Simpson, 1948	–	X	–	–	–	–	–	–	–	–	–	–
Amphidolops serrula Ameghino, 1902	X	–	–	–	–	–	–	–	–	–	–	X
Eudolops tetragonus Ameghino, 1897	X	–	–	–	–	–	–	–	–	–	–	X
E. caroliameghinoi (Ameghino, 1903)	–	–	–	–	X	–	–	–	–	–	–	–
Utaetus buccatus Ameghino, 1902	X	–	–	–	–	–	–	–	–	–	?X	–
U. lenis (Ameghino, 1902)	X	–	–	–	–	–	–	–	–	–	–	–
U. deustus Ameghino, 1902	X	–	–	–	–	–	–	–	–	–	–	–
"*Pseudostegotherium*" *chubutanum* Ameghino, 1902	X	–	–	–	–	–	–	–	–	–	–	–
Prostegotherium notostylopianum Ameghino, 1902	X	–	–	–	–	–	–	–	–	–	–	–
Adiantoides magnus Cifelli and Soria, 1983	–	X	–	–	–	–	–	–	–	–	–	–
Sparnotheriodon epsilonoides Soria, 1980	–	X	–	–	–	–	–	–	–	–	–	–
Didolodus multicuspis Ameghino, 1897	X	–	–	–	–	–	–	–	–	–	–	–
D. latigonus (Ameghino, 1902)	–	–	–	–	–	X	–	–	–	–	–	–
D. minor Simpson, 1948	–	X	–	–	–	–	–	–	–	–	–	–
Paulogervaisia inusta Ameghino, 1901	X	–	–	–	–	–	–	–	–	–	–	–
P. porca (Ameghino, 1901)	X	–	–	–	–	–	–	–	–	–	–	–
P. mamma (Ameghino, 1901)	X	–	–	–	–	–	–	–	–	–	–	–
Proectocion argentinus Ameghino, 1904	X	–	–	–	–	–	–	–	–	–	–	–
P. precisus Ameghino, 1904	X	–	–	–	–	–	–	–	–	–	–	–
Enneoconus parvidens Ameghino, 1901	–	–	–	–	–	X	–	–	–	–	–	–
Asmithwoodwardia subtrigona Ameghino, 1901	–	X	–	–	–	–	–	–	–	–	–	–
Ernestokokenia nitida Ameghino, 1901	X	–	–	–	–	–	–	–	–	–	–	–
E. patagonica (Ameghino, 1901)	–	–	–	X	–	–	–	–	–	–	–	–
Victorlemoinea labyrinthica Ameghino, 1901	–	–	–	–	–	X	–	–	–	–	–	–
V. emarginata Ameghino, 1901	–	–	–	–	–	X	–	–	–	–	–	–
V. sp. indet.	–	X	–	–	–	–	–	–	–	–	–	–
Ernestohaeckelia acutidens Ameghino, 1901	–	–	–	–	–	X	–	–	–	–	–	–
Anisolambda fissidens Ameghino, 1901	X	X	–	–	–	–	–	–	–	–	–	–
A. adunca (Ameghino, 1901)	–	–	–	–	–	X	–	–	–	–	–	–
A. amel Simpson, 1948	–	X	–	–	–	–	–	–	–	–	–	–
Guilielmofloweria plicata Ameghino, 1901	X	–	–	–	–	–	–	–	–	–	–	–
Henricosbornia lophodonta Ameghino, 1901	?X	X	–	–	–	–	X	–	–	–	–	–
H. ampla (Ameghino, 1904)	–	–	–	–	–	–	X	–	–	–	–	–
Othnielmarshia lacunifera Ameghino, 1901	–	X	–	–	–	–	X	–	–	–	–	–
Peripantostylops minutus (Ameghino, 1901)	–	X	–	–	–	–	X	–	–	–	–	–
Notostylops murinus Ameghino, 1897	X	–	–	X	–	–	–	–	–	–	X	–
N. pendens (Ameghino, 1901)	–	X	–	–	–	–	X	–	–	–	–	?X
N. appressus (Ameghino, 1902)	–	X	–	–	–	–	–	–	–	–	–	–
N. pigafettai Simpson, 1948	–	–	–	–	–	–	–	X	–	–	–	–
Homalostylops parvus (Ameghino, 1897)	X	–	–	–	–	–	–	–	–	–	–	–
Homalostylops sp. nov.?	–	X	–	–	–	–	–	–	–	–	–	–
Edvardotrouessartia sola Ameghino, 1901	–	X	–	–	–	–	X	–	–	–	–	–

TABLE 1—(*Continued*)

Species	Localities[b]											
	1	2	3	4	5	6	7	8	9	10	11	12
Maxschlosseria praeterita Ameghino, 1901	–	–	–	–	–	–	X	–	–	–	–	–
M. minima (Ameghino, 1897)	–	–	–	–	–	–	X	–	–	–	–	–
M. rusticula (Ameghino, 1901)	–	–	–	–	–	–	X	–	–	–	–	–
M. consumata (Ameghino, 1901)	–	X	–	–	–	–	X	–	–	–	–	–
Oldfieldthomasia debilitata (Ameghino, 1901)	X	–	–	–	X	X	–	–	–	–	–	–
O. parvidens Ameghino, 1901	X	–	–	–	–	–	–	–	–	–	–	–
O. sp. indet.	–	–	–	–	–	–	–	–	–	–	X	X
Ultrapithecus rutilans Ameghino, 1901	X	–	–	–	–	–	–	–	–	–	–	–
Acoelodus oppositus Ameghino, 1897	X	–	–	–	–	–	–	–	–	–	–	–
"*A.*" *proclivus* Ameghino, 1902	X	–	–	–	–	–	–	–	–	–	–	–
Paginula parca Ameghino, 1901	X	–	–	–	–	–	X	–	X	–	–	–
Archaeopithecus rogeri Ameghino, 1897	X	–	–	–	–	–	–	–	–	–	–	–
Acropithecus rigidus (Ameghino, 1901)	–	X	–	–	–	–	X	–	–	–	–	–
Notopithecus adapinus Ameghino, 1897	X	–	–	X	–	X	–	–	–	X	–	X
Antepithecus brachystephanus Ameghino, 1901	X	–	–	–	–	–	–	–	–	–	?X	–
Transpithecus obtentus Ameghino, 1901	X	–	–	–	–	–	–	–	–	–	–	–
Eohyrax rusticus Ameghino, 1901	–	–	–	–	–	X	–	–	–	–	–	–
E. isotemnoides Ameghino, 1904	X	–	–	–	–	–	–	–	–	–	?X	–
E. praerusticus Ameghino, 1902	X	–	–	–	–	–	–	–	–	–	–	–
Pleurostylodon modicus Ameghino, 1897	X	–	–	X	–	–	–	–	–	X	–	–
P. similis Ameghino, 1901	–	X	?X	–	–	–	–	–	–	–	–	–
?*P. recticrista* (Ameghino, 1904)	–	–	–	–	–	X	–	–	–	–	–	?X
Anisotemnus distentus (Ameghino, 1901)	X	–	–	–	–	X	X	–	X	X	–	–
Acoelohyrax complicatissimus (Ameghino, 1904)	X	–	–	–	–	–	–	–	–	–	–	–
Isotemnus primitivus Ameghino, 1897	X	X	–	–	–	X	–	–	–	–	–	X
I. latidens (Ameghino, 1901)	–	–	–	–	–	X	–	–	–	–	–	–
Thomashuxleya rostrata Ameghino, 1901	X	–	–	X	–	–	–	–	–	–	–	–
Thomashuxleya externa Ameghino, 1901	–	X	X	–	–	X	X	–	–	–	–	–
Scaglia kraglievichorum Simpson, 1957	–	X	–	–	–	–	–	–	–	–	–	–
Trigonostylops wortmani Ameghino, 1897	X	?X	–	X	–	X	–	–	–	–	X	–
Albertogaudrya unica Ameghino, 1901	X	–	–	X	X	–	–	–	X	–	–	X
A. sp. indet.	–	X	–	–	–	–	–	–	–	–	–	–
Carolozittelia tapiroides Ameghino, 1901	–	–	–	–	–	X	–	–	–	–	–	–
Florentinoameghinia mystica Simpson, 1932	–	X	–	–	–	–	–	–	–	–	–	–

[a] Data from Simpson, 1948, 1964, 1967a, 1967b, and personal observations.

[b] Localities: 1, Cohué Huapí (Gran Barranca); 2, Cañadón Vaca (excluding faunule 6); 3, Cañadón Hondo; 4, Colhué Huapí norte; 5, Cerro Blanco; 6, Río Chico oeste; 7, Río Chico este; 8, Cerro del Humo; 9, Cerro Negro; 10, Pico Salamanca; 11, Cañadón Lobo; 12, Tapera de López.

Patagonia lie at the base of a series of mainly pyroclastic sediments, the "tobas de Sarmiento" (Sarmiento tuffs) of Feruglio (1938). The Sarmiento tuffs, or "Sarmiento group" (a term which has been used both formally and informally), also includes mammal-bearing beds of Mustersan, Deseadan, and Colhuehuapian age (all four faunas are found in superposition at the Gran Barranca south of Lago Colhué Huapí) and are bounded below by the terrestrial sandstones/claystones of the Río Chico Formation and above by the marine Monte León ("Patagonia") Formation, respectively. Largely loessic in origin (Spalletti and Mazzoni, 1977), the "Sarmiento group" is nonetheless highly varied in lithology and complex in internal structure (Simpson, 1940). Despite the long span of time represented, it includes many hiatuses and is relatively thin, perhaps 150 to 190 m thick (Feruglio, 1949). Simpson (1940) applied the geographic South American land mammal age names (see Simpson, 1933) to the rock units containing the respective

mammal faunas, based in part on well marked erosional planes between them. The term "Casamayor" was proposed as a stage, however, and has never been defined as a rock unit. (See Savage, 1962; Pascual et al., 1965; and Simpson, 1971, for discussions regarding the confusion of lithostratigraphic with chronostratigraphic and geochronologic terms.)

Based on detailed analysis of a 114.5-m thick section measured at km 163 of the railway between Comodoro Rivadavia and Sarmiento (central Chubut, fig. 2), Spalletti and Mazzoni (1977) recognized three sedimentary cycles in beds of the "Sarmiento group." They believed that these cycles correspond, respectively, to the Casamayoran, Mustersan, and Deseadan land mammal ages. The sedimentary cycles are characterized by varying percentages of bentonites, tuffs, "homeoconglomerates," and paleosols; they were correlated to the respective land mammal ages according to apparently correlative environmental changes in faunal composition (Pascual and Odreman Rivas, 1971). Based on study of a nearby section (8.5 km north of km 162 on the Comodoro Rivadavia to Sarmiento railway), Spalletti and Mazzoni later (1979) concluded that the "Sarmiento group" constitutes a lithologic entity and defined it as a formation with three members. According to these authors, the lowest, or Gran Barranca Member, conformably overlies the Río Chico Formation, lacks vertical cyclicity, and contains mammalian fossils of Casamayoran age. An erosional contact separates the Gran Barranca Member from the overlying Puesto Almendra Member. The Puesto Almendra Member consists of alternating tuffs and conglomerates, contains mammalian fossils of Deseadan age near its base, and includes a basalt radiometrically dated at 35 ma. The uppermost, or Colhuehuapi Member, concordantly overlies the Puesto Almendra Member and contains fossils of Colhuehuapian age. Spalletti and Mazzoni (1979) indicated that the Gran Barranca Member probably corresponds to the lower and middle cycles of their earlier (1977) section and that the lower part of the Puesto Almendra Member may correspond to the upper cycle, but they stressed that lateral changes in lithology and bed thickness preclude direct correlation of strata between their sections.

Andreis (1977) proposed separate lithostratigraphic names for "Sarmiento group" sediments of Casamayoran and Deseadan age in the Cañadón Hondo region (see also Simpson, 1935; Schaeffer, 1947). Andreis proposed the name Cañadón Hondo Formation for the Casamayoran beds, which in this area overlie the Visser Member of the Río Chico Formation (Andreis et al., 1975) with angular unconformity. He referred to the unconformably overlying Deseadan sediments as the El Sol Formation. Andreis (1977) proposed these names as replacements for those adopted by Simpson (1940) in the belief that names such as "Deseado Formation" and "Casamayor Formation" confuse lithostratigraphic with chronostratigraphic terms (sensu Hedberg, 1976). Unlike the earlier terminology, the lithostratigraphic units proposed by Andreis (1977) are defined as such, but their status as replacements (as well as the status and circumscription of the names used by Simpson) remains unclear or dubious. The areal extent of the "El Sol Formation" was not given; the Cañadón Hondo Formation" was defined as a strictly local entity, thinning to the south and not occurring to the west of the Río Chico. Thus, if the latter is to be recognized as valid, new names will have to be proposed for correlative strata in the region of Cañadón Vaca and probably elsewhere as well. In light of these confusions and unclear definitions, I use the term "Sarmiento group," in an informal sense, to refer to all sediments of Casamayoran to Colhuehuapian age in central Patagonia.

CASAMAYORAN LOCAL FAUNAS AND BIOSTRATIGRAPHY

Simpson (1948, 1967b, and references therein) revised the mammals from the Casamayoran of Patagonia and published locality data for such of the Ameghino type specimens as that information was available (1967a). Table 1 presents a revised list of mammal species from the Casamayoran of Patagonia, based largely on these publications but with some unpublished additions

and emendations (Savage and Russell, 1983, pp. 86–88, list a composite Casamayoran fauna). None of these is definitely known from the Riochican, but a number of them belong to genera also known from the *Ernestokokenia chaishoer* zone (?transitional Riochican-Casamayoran) of the Bajo de la Palangana upper sandstone and the *Kibenikhoria* Riochican zone of the Cañadón Hondo sandstone (Simpson, 1935).[3] There are no species and, with a few dubious exceptions, no genera known from the Casamayoran or Mustersan and later faunas. These exceptions include the virtually indistinguishable large isotemnids *Thomashuxleya* and *Periphragnis,* from the Casamayoran and Mustersan, respectively,[4] and the aberrant ?didolodontoid *Adiantoides,* now known by a species from the Casamayoran of Cañadón Vaca in addition to the genotype from the Divisaderan (Cifelli and Soria, 1983).

Most of Carlos Ameghino's Casamayoran localities and a number of others were visited and collected by the Scarritt Patagonian Expeditions. The collections so made are large and, in most cases, well documented stratigraphically, and therefore offer an unparalleled opportunity to determine the contents, superposition, and age relationships of the various Casamayoran local faunas. The two largest samples were collected at the Gran Barranca, south of Lago Colhué Huapí, and at Cañadón Vaca, west of the Río Chico, central Chubut (fig. 1). Because these samples are large, diverse, rather dissimilar, and span relatively great stratigraphic intervals, initial comparison is limited to the two faunas.

[3] Cabrera (1936; cited from Simpson, 1948, p. 126 and 1967a, p. 71, and not seen by me) assigned some Riochican specimens to Casamayoran species; these identifications were considered doubtful by Simpson in the works cited (have not seen the materials). Pascual (in Marshall et al., 1983, and personal commun.) reports the presence of typically Casamayoran species in the ?transitional Riochican-Casamayoran Bajo de la Palangana upper sandstone fauna.

[4] Simpson, 1967b, p. 163, comments: "*Periphragnis* is so closely similar to *Thomashuxleya* that the generic diagnosis [of *Periphragnis*] is not clear-cut and if the two were of the same age they would perhaps be considered generically identical."

Gran Barranca

One of the most important fossil mammal localities in the world, the Gran Barranca south of Lago Colhué Huapí, Chubut (fig. 1) was discovered by Carlos Ameghino in 1895. Here, the four mammal faunas of the "Sarmiento group"—Casamayoran, Mustersan, Deseadan, and Colhuehuapian—lie together in a single superposed sequence. Detailed sections through the "Sarmiento group" sediments in this vicinity were described by Spalletti and Mazzoni (1977, 1979). Fossil mammals collected in the region by the Scarritt Expeditions were keyed to measured sections; those profiles incorporating significant Casamayoran assemblages are shown in figures 3–5 and their approximate locations are given in figure 2. The only direct lithologic correlation between all sections is a marker horizon traced throughout[5] by Simpson ("marker bed" of figures 3–5). This is a tuff, several meters in thickness, and usually massive and white with a pink hue in a few exposures. It almost always forms a prominent salient, and many fossils of Casamayoran age were collected from it. This tuff may be equivalent to level "P11" of Spalletti and Mazzoni (1977, p. 265) and perhaps also to the "primer nivel fosilífero" of Spalletti and Mazzoni (1979, p. 273). In all of the profiles which include the lower parts of the stratigraphic column, about 45 m of alternating tuffs and bentonitic clays (McCartney, 1933), containing Casamayoran fossils, intervene between the marker tuff and partially indurated tuffs and clays of the "Sarmiento group," the "argiles fissilaires" of Ameghino (McCartney, 1934). Fossils have not been found in these diagenetically altered sediments. Although no continuous section is exposed, Simpson estimated these opalized beds to range from 35 to 45 m in thickness; they lie in apparent concordance on the alternating sandstones and detrital claystones of the Río Chico Formation. Fossils were not recovered from the Río Chico Formation in this vicinity by the Scarritt Expeditions, but Riochican mammals have since been discovered here

[5] This horizon has been relocated by subsequent workers (Marshall, personal commun.).

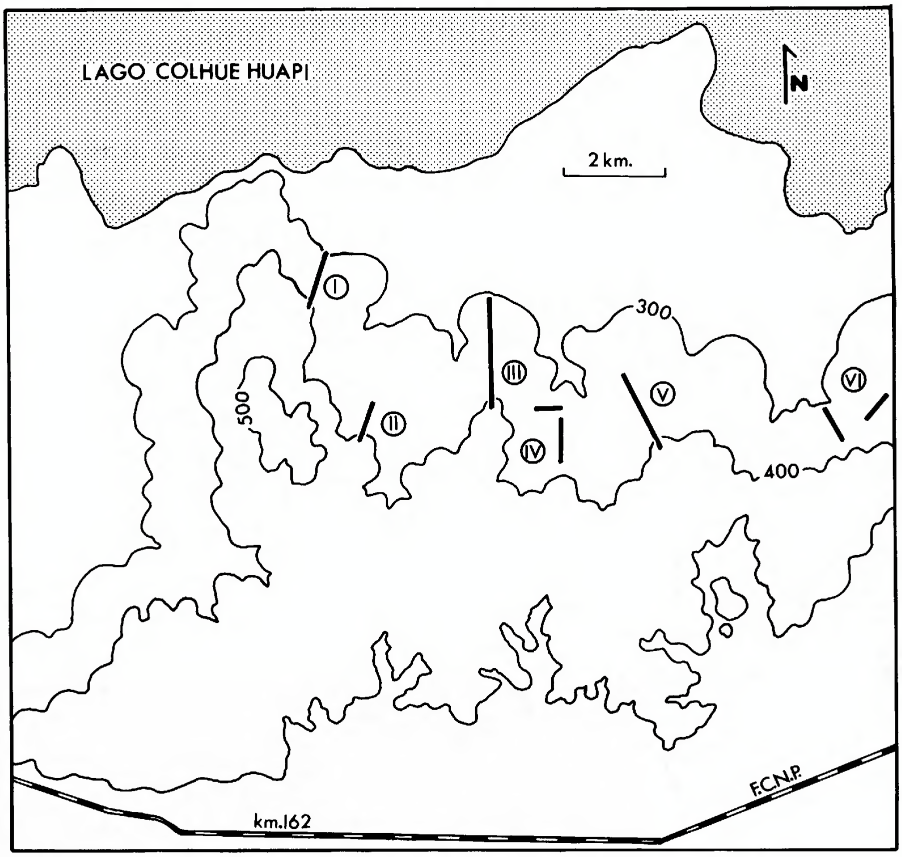

FIG. 2. Details of black rectangular area on figure 1, showing approximate locations of sections measured at the Gran Barranca, south of Lago Colhué Huapí (figs. 3–5) by G. G. Simpson. Contours represent meters above sea level.

(Pascual and Bond, 1981). Above the marker horizon, about 20 more meters of variously colored alternating tuffs and bentonitic claystones containing Casamayoran fossils occur. At this point in profiles I and II (and other measured sections not included here) a basal conglomerate and channel series begins; traced eastward, this grades into an impure tuff which may or may not be unconformable with overlying strata (profile V).

Casamayoran mammals from the Gran Barranca were recovered from numerous horizons in the "Sarmiento group," from about 10 m above the silicified tuffs and claystones to (and including) the base of the channel series, and were found in great abundance in the marker horizon. The maximum recorded vertical distribution of Casamayoran fossils at the Gran Barranca is therefore about 60 m. The stratigraphically highest Casamayoran mammals are registered on profile V (fig. 5), about 20 m above the base of the marker bed and in an indurated, manganese-bearing pink tuff. This tuff may be unconformable with underlying beds; Simpson observed it to grade laterally into the channel series noted above. (The few specimens from the site in question, no. 15, are somewhat rolled and may have been reworked.) With the exception of *Periphragnis exauctus*, the composition of this highest assemblage is Casamayoran. To the west, on profile I (fig. 3), a typically Mustersan assemblage (site 4), including *Distylophorus alouatinus*, *Periphragnis exauctus*, *Rhyphodon* sp., and *Astraponotus* sp., occurs in the base of the channel series and at a level slightly higher than that of site 15; Mustersan fossils (pertaining to the no-

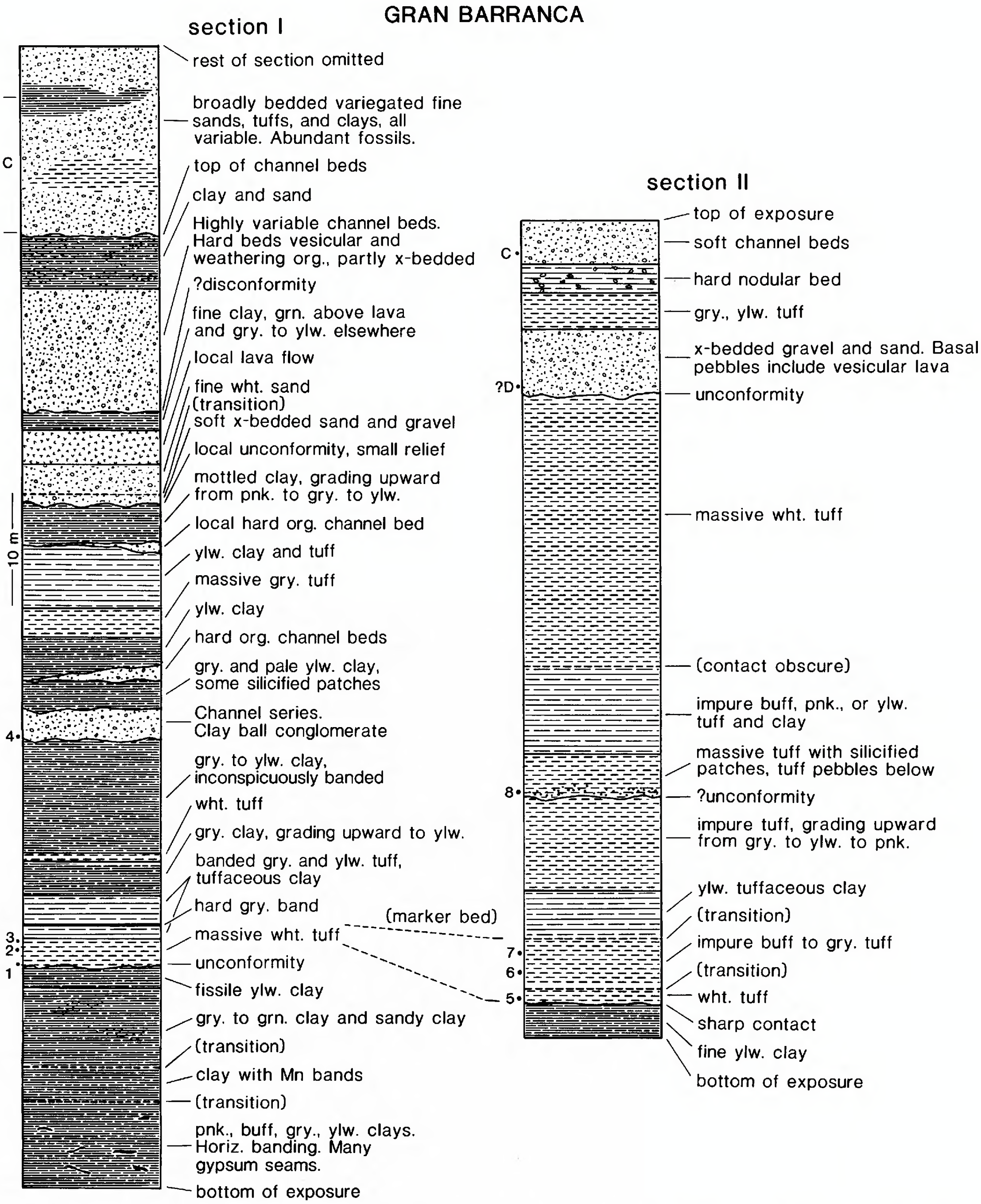

FIG. 3. Measured sections I and II at the Gran Barranca south of Lago Colhué Huapí, redrawn after fieldnotes of G. G. Simpson. Numbers at left indicate Mustersan and Casamayoran fossil horizons or sites listed in table 2. See figure 2 for approximate locations of sections. ?D, faunule of probable Deseadan age; C, faunule of Colhuehuapian age.

tohippid genus *Eomorphippus*; sites 16 and 17) are recorded also in section V, where they were collected both above and below an unconformity nearly 20 m higher than site 4. The channel series is thus taken here to represent a lithologic change and, probably, hia-

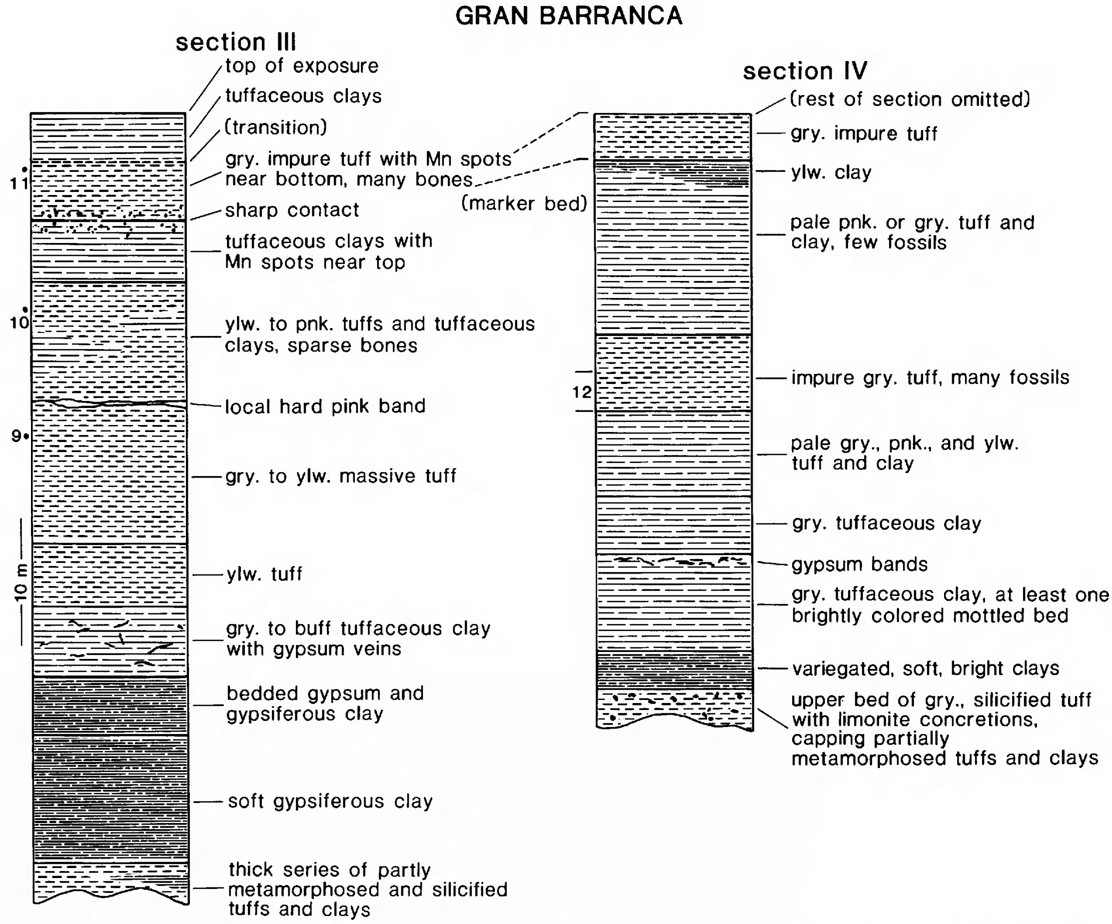

FIG. 4. Measured sections III and IV at the Gran Barranca south of Lago Colhué Huapí, redrawn after fieldnotes of G. G. Simpson. Numbers at left indicate Casamayoran fossil horizons or sites listed in table 2. See figure 2 for approximate locations of sections.

tus, coinciding with the distribution of Casamayoran and Mustersan fossils at the Gran Barranca. Fossils have unfortunately not been recovered from areas which may have had more continuous deposition or less erosion during the time represented by this hiatus.

Approximately 20 m of sediments, the same distance as that between the marker horizon and the channel series, also occur between Spalletti and Mazzoni's (1979, fig. 2) "primer nivel fosilífero" and the unconformity separating their Gran Barranca and Puesto Almendra members of the "Sarmiento Formation." It is thus possible that the "primer nivel fosilífero" is a correlate of the marker horizon and the Gran Barranca-Puesto Almendra unconformity is a correlate of the base of the channel beds described in the present paper. The lower part of the Puesto Almendra Member, consisting largely of conglomerates, was considered by these authors to be early Oligocene in age because it includes a basalt flow, possibly correlative to that at Cerro Blanco dated by Marshall et al. (1977) at 35 ma. and because it contains a Deseadan fauna. Sediments of Mustersan age were therefore probably not deposited (or were removed prior to renewed deposition during the Deseadan) in the area studied by Spalletti and Mazzoni (1979). In another section, these authors had previously (1977) recorded Casamayoran fossils from a level P11 (possibly equivalent to the marker horizon, as noted above); a marked unconformity sep-

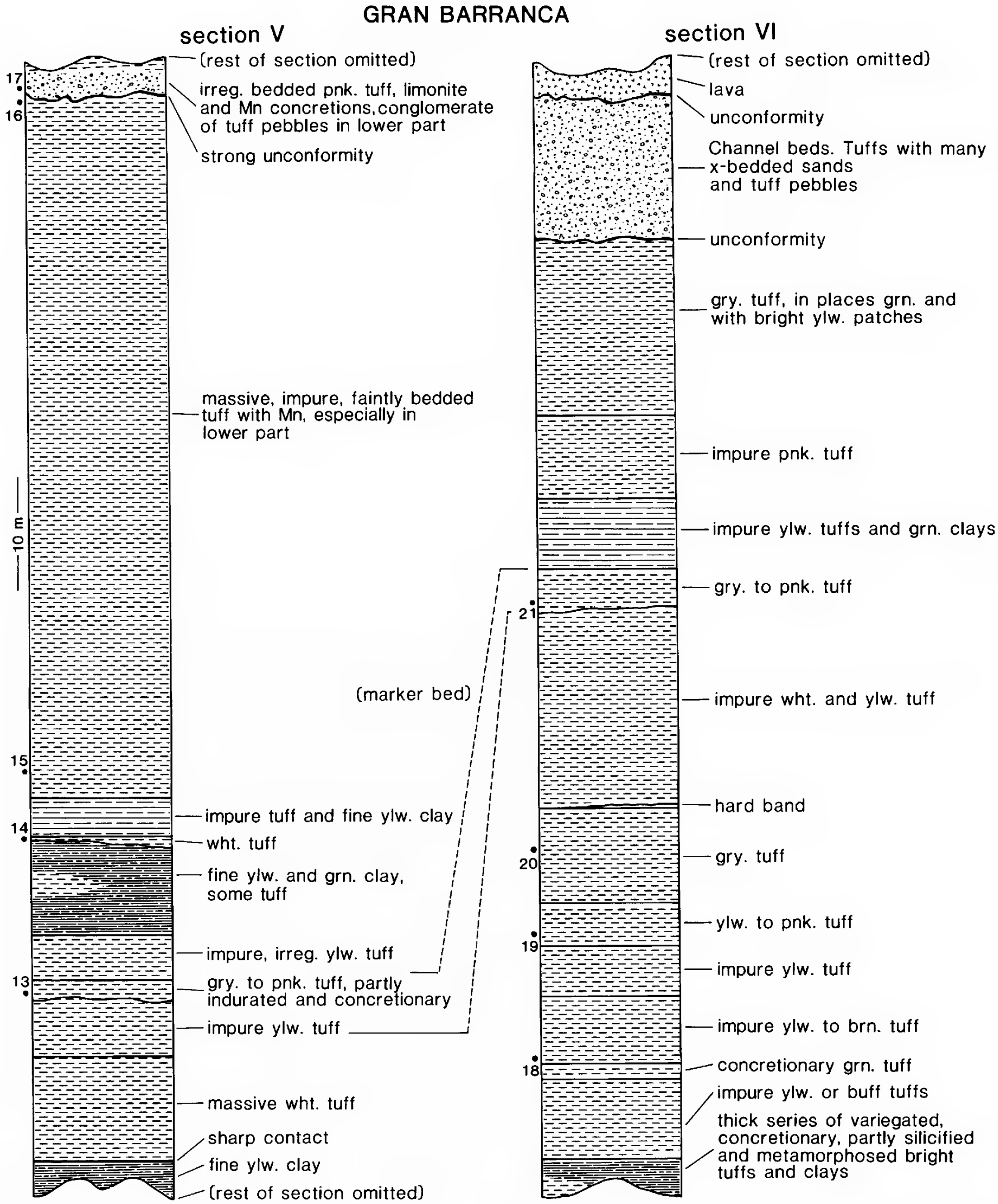

FIG. 5. Measured sections V and VI at the Gran Barranca south of Lago Colhué Huapí, redrawn after fieldnotes of G. G. Simpson. Numbers at left indicate Mustersan and Casamayoran fossil horizons or sites listed in table 2. See figure 2 for approximate locations of sections.

arates their horizons P14 and P15 approximately 20 m above level P11. This is an appropriate level to correspond to the unconformity and channel beds recognized here, although it should be noted that Spalletti and Mazzoni (1977) did not observe con-

TABLE 2

Composition of Gran Barranca Faunules[a]

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
Casamayoran																					
Caroloameghinia mater	–	–	–	–	–	–	–	–	–	–	–	X	–	–	–	–	–	–	–	–	–
Patene coluapiensis	–	–	–	–	–	–	–	–	–	–	–	X	–	–	–	–	–	–	–	–	–
Polydolops thomasi	–	–	–	–	–	–	–	–	–	–	X	X	–	–	–	–	–	–	–	–	–
Amphidolops serrula	–	–	–	–	–	–	X	–	–	–	–	–	–	–	–	–	–	–	–	–	–
A. sp. indet.	–	–	–	–	–	X	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Utaetus buccatus	–	–	–	–	–	–	–	–	–	–	–	X	–	–	–	–	–	–	–	–	–
U. sp. indet.	–	–	–	–	–	X	–	–	–	X	–	–	–	–	–	–	–	–	–	–	–
Didolodus multicuspis	–	–	–	–	X	–	–	–	–	–	–	X	–	–	–	–	–	–	–	–	–
Ernestokokenia nitida	–	–	–	–	–	X	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Henricosbornia lophodonta	–	–	–	–	?X	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Notostylops murinus	–	–	–	–	X	X	X	–	–	X	X	X	–	–	–	–	–	–	–	–	–
N. sp. indet.	–	–	–	–	–	–	–	X	–	–	–	–	–	–	X	–	–	X	–	–	–
Homalostylops parvus	–	–	–	–	–	–	–	–	–	–	–	–	–	–	X	–	–	–	–	–	–
H. sp.	–	–	–	–	–	–	–	–	–	–	–	X	–	–	–	–	–	–	–	–	–
Oldfieldthomasia debilitata	–	–	–	–	X	X	X	–	–	–	X	X	–	–	–	–	–	–	X	–	–
Ultrapithecus rutilans	–	–	X	–	X	X	–	–	–	–	X	–	–	–	X	–	–	–	–	–	–
Notopithecus adapinus	–	–	–	–	–	X	–	–	–	–	X	X	–	–	–	–	–	?X	–	–	–
N. a. adapinus	–	–	X	–	–	X	X	–	–	–	–	–	–	–	–	–	–	–	–	–	–
N. a. reduncus	–	–	–	–	–	–	–	–	–	–	–	X	–	–	–	–	–	–	–	X	–
N. sp. indet.	X	–	–	–	X	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Antepithecus brachystephanus	–	–	–	–	X	X	X	X	–	–	X	–	–	–	–	–	–	–	–	–	–
Transpithecus ?obtentus	–	–	–	–	–	–	–	–	–	–	–	X	–	–	–	–	–	–	–	–	–
Eohyrax isotemnoides	–	–	–	–	X	X	X	–	–	–	–	–	–	–	–	–	–	–	–	–	–
E. sp. indet.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	X	–	–	–	–	–	–
Pleurostylodon modicus	–	–	X	–	X	X	X	–	–	X	X	–	X	–	–	–	–	–	X	–	–
P. sp. indet.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	X	–	–	–	–
Anisotemnus distentus	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	X	–	–	–	–
A. sp. indet.	–	X	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Isotemnus primitivus	–	–	–	–	–	–	–	–	–	–	–	–	–	X	–	–	–	–	–	–	–
Thomashuxleya rostrata	X	–	–	–	–	–	–	–	–	–	X	–	–	–	–	–	–	X	–	–	–
Trigonostylops wortmani	–	X	–	–	–	?X	?X	–	–	–	–	–	–	–	–	–	–	X	–	–	–
Albertogaudrya unica	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	X	–	–	–
A. sp. indet.	–	–	–	–	–	X	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–

TABLE 2—(*Continued*)

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
Mustersan																					
Periphragnis exauctus	–	–	–	X	–	–	–	–	–	–	–	–	–	–	X	–	–	–	–	–	–
Distylophorus alouatinus	–	–	–	X	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Rhyphodon sp. indet.	–	–	–	X	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Eomorphippus obscurus	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	X	–	–	–	–	–
?E. pascuali	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	X	X	–	–	–	–
Astraponotus sp. indet.	–	–	–	X	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–

[a] Numbers refer to sites or levels in measured sections of figures 3, 4, and 5. Data from the collections of the Scarritt Patagonian Expeditions only; occurrences not known by precise stratigraphic horizon ignored. See table 1 for author and date of species.

glomerates at this point in their section. If these correlations are correct, the distribution of faunas presented herein corroborates Spalletti and Mazzoni's (1977) association of sedimentary cycles to the Casamayoran, Mustersan, and Deseadan land mammal ages, respectively.

The composition of the Gran Barranca assemblages is given in table 2, and the stratigraphic ranges of identified mammals from the Gran Barranca, taken from profiles I–VI, are combined in figure 6. Although local variations in lithology and bed thicknesses preclude exact correlation, the thicknesses of strata between the marker horizon and the channel series unconformity and the diagenetically altered tuffs and claystones are approximately the same in all sections where they are recorded. Therefore, there is no reason to believe that the relative vertical position of the various assemblages would be different were the sections more lithologically correlatable.

Many species are known by only one or a few specimens. Of the more abundant species (those assumed to be most likely to be sampled at any given horizon if they were originally present), *Notostylops murinus, Oldfieldthomasia debilitata, Notopithecus adapinus, Pleurostylodon modicus,* and *Trigonostylops ?wortmani* are not known from levels above the marker bed, while *Homalostylops parvus, Ultrapithecus rutilans,* and *Antepithecus brachystephanus* are not known from below that horizon. These distributions may be significant because most of the species listed are relatively abundant where they occur. Nonetheless, the assemblages are unevenly distributed throughout the section and sampling is poor for large parts of it, especially above the marker horizon. The distribution of specimens in the combined section is shown in figure 7. About 68 percent of identified materials derived from or near the marker tuff (sites 1, 2, 3, 5, 6, 7, 11, 13, 21); 24 percent came from scattered levels below that stratigraphic interval (sites 9, 10, 12, 18, 19, 20); and the remainder from above it (sites 8, 14, 15). The possibility that species absences from the upper or lower part of the section are the result of sampling inadequacies may be evaluated by determining the

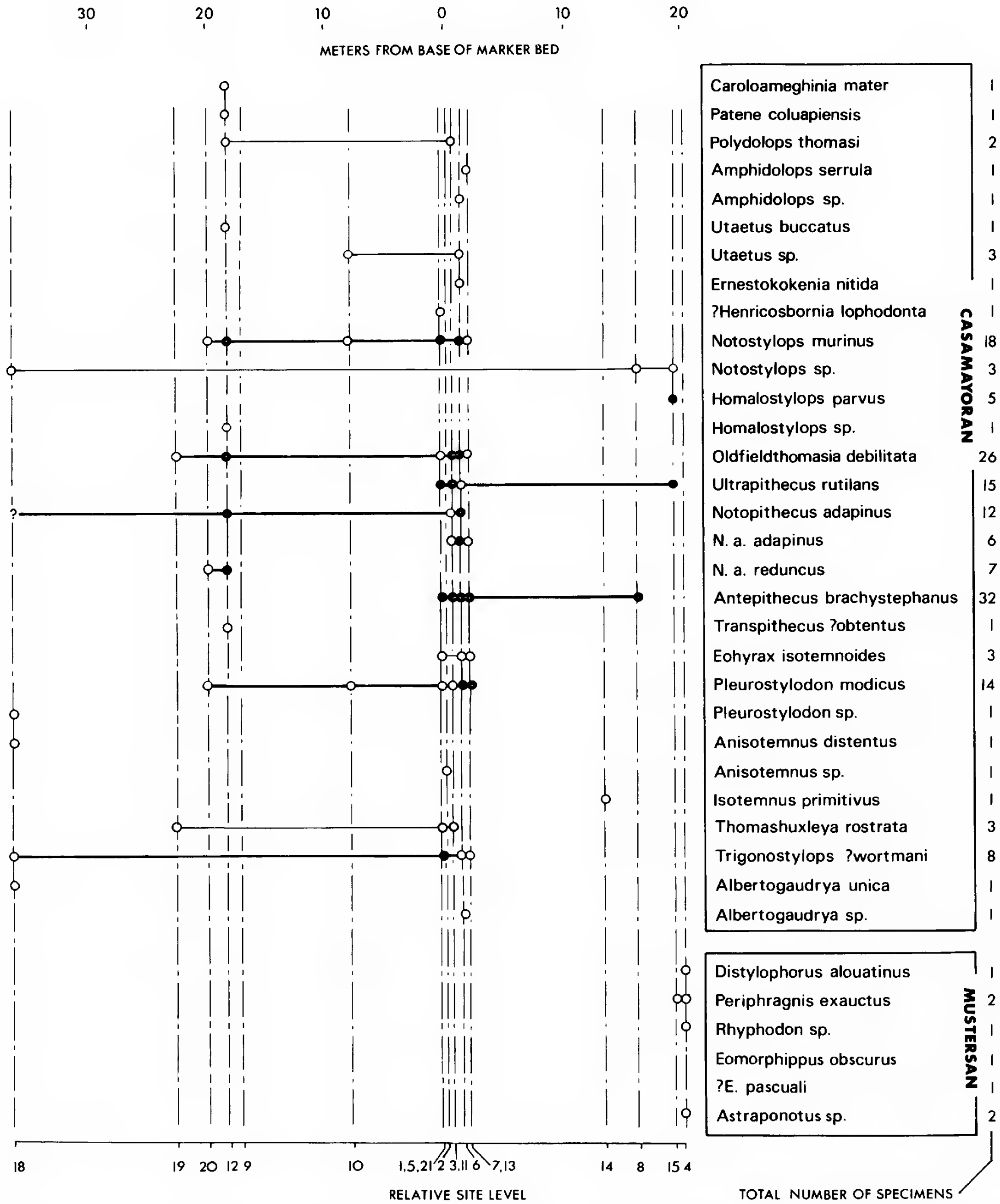

FIG. 6. Abstracted stratigraphic distributions of Casamayoran and Mustersan mammals at the Gran Barranca south of Lago Colhué Huapí, combining distributional data from measured sections I–VI (figs. 3–5). The base of the marker horizon, traced throughout, is the lithostratigraphic datum for this composite. Numbers at right denote fossil horizons or sites listed in table 2 and indicated on figures 3–5 (Mustersan faunules nos. 16 and 17 are omitted). Open circles: three or fewer specimens of that species recovered from a given horizon; closed circles, more than three. Light horizontal lines: less than a total of five specimens placed stratigraphically for that species; heavy lines, five or more specimens. Other taxa known from the Gran Barranca locality region cannot be placed precisely in this stratigraphic column.

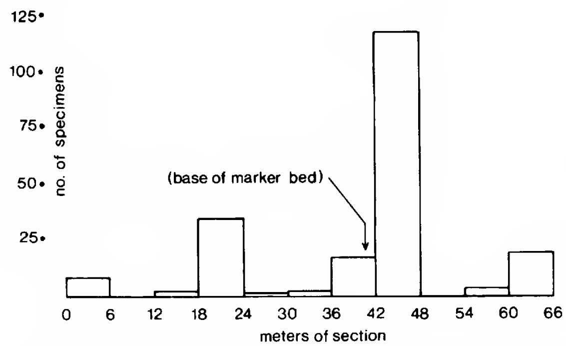

FIG. 7. Histogram showing stratigraphic distribution with respect to relative abundance of fossil mammal specimens recovered by the Scarritt Patagonian Expeditions at the Gran Barranca. As with figure 6, the base of the marker horizon is used as a lithostratigraphic datum plane; numbers at left indicate total number of specimens recovered from each 6-m interval.

relative abundance of each species where it is found and determining the probability that its nonrepresentation elsewhere is due to chance. Using the binomial distribution, population parameters are determined as follows:

P (abundance of occurrence for a given species)

$$= \frac{n}{N + N_x}$$

S (standard deviation)

$$= \sqrt{(N + N_x)P(1 - P)}$$

p (predicted abundance value for sample in which that species is absent)

$$= PN_x;$$

where n = number of specimens pertaining to that species, N = the total number of specimens from the marker horizon (sites 1, 2, 3, 5, 6, 7, 11, 13, 21), and N_x = the total number of specimens from above (sites 8, 14, 15) or below (sites 9, 10, 12, 18, 19, 20) the marker horizon. (The value used depends on the distribution of the species in question.) The probability that a given species absence is the result of sampling inadequacy (i.e., the probability that it was present but no specimens were found) is determined by using a normal approximation to the binomial distribution:

$$Z = \frac{X - PN_x}{(N + N_x)P(1 - P)},$$

where X is the binomial random variable (in this case, equal to zero because it is absence data which are being evaluated), and Z is the standard normal random variable $\frac{(X - \mu)}{\sigma}$.

The probabilities of species absences due to chance are given in table 3. These probabilities are not great for those species outside the lower part of the section (where sampling is good), especially for otherwise abundant species such as *Antepithecus brachystephanus*. The higher values for those absent from levels above the marker horizon reflects the smaller sample size from that portion of the

TABLE 3
Distributional Significance of the More Abundant Gran Barranca Species[a,b]

Species	n	P	s	p	Z	A
Notostylops murinus	18	.099	4.02	1.58	−.39	.3483
Oldfieldthomasia debilitata	26	.144	4.72	2.30	−.49	.3121
Notopithecus adapinus	25	.138	4.64	2.21	−.48	.3156
Pleurostylodon modicus	14	.077	3.59	1.23	−.34	.3669
Trigonostylops ?wortmani	8	.044	2.76	0.70	−.25	.4013
Homalostylops parvus	5	.033	2.19	1.55	−.71	.2389
Ultrapithecus rutilans	15	.100	3.67	4.70	−1.28	.1003
Antepithecus brachystephanus	32	.213	5.01	10.01	−2.00	.0228

[a] N (number of specimens from marker horizon localities, nos. 1, 2, 3, 5, 6, 7, 11, 13, 21) = 134; N_1 (number of specimens from the upper localities, nos. 8, 14, 15) = 16; N_2 (number of specimens from the lower localities, nos. 9, 10, 12, 18, 19, 20) = 47.
[b] n = no. of specimens; P = probability of occurrence; s = standard deviation; p = predicted value of occurrence; Z = value of transformed normal random variable; A = area of normal curve for $Z \leq 0$.

TABLE 4
Distributional Significance of *Notopithecus adapinus* Subspecies[a]

Subspecies	n	P	s	p	Z	A
Notopithecus adapinus adapinus	6	.045	2.39	1.58	−.66	.2546
Notopithecus adapinus reduncus	5	.200	2.37	24.60	−10.40	.0000

[a] See table 3 for abbreviations. N (marker horizon localities) = 134 − 11 *Notopithecus adapinus* specimens = 123; N_1 (number of specimens from localities 12, 20) = 35.

section, and are greatest for the rarer forms such as *Trigonostylops ?wortmani.*

The taxonomy and relative stratigraphic positions of the subspecies of *Notopithecus adapinus* have been discussed by Simpson (1967b, pp. 78–80). Specimens recognizable as belonging to both subspecies, *N. a. adapinus* and *N. a. reduncus,* have not been found at the same horizon. Rather, *N. a. adapinus* is restricted to localities at the level of the marker horizon, whereas *N. a. reduncus* occurs only at two levels (sites 12, 20) well below that horizon (fig. 6). As before, the probabilities that these observed distributions are the result of chance nonrepresentation may be determined by a normal approximation to the binomial distribution (table 4). The gracile-jawed (?a primitive condition) *N. a. reduncus,* rather abundant at sites 12 and 20, was almost certainly never present at the marker horizon; there is an approximately 25 percent chance that the absence of *N. a. adapinus* at localities 12 and 20 is a result of sampling error.

Cañadón Vaca

Large samples of Casamayoran mammals were recovered by the first Scarritt Patagonian Expedition also at Cañadón Vaca, west of the Río Chico and approximately 60 km northeast of the localities south of Lago Colhué Huapí (see fig. 1). "Sarmiento group" rocks, consisting of variously colored alternating tuffs and bentonitic claystones, are exposed on the north side of the cañadón. Conglomeritic sandstone and an impure tuff occur at the base of the "Sarmiento group"; these overlie with a sharp but planar contact the gray shales (with no observable bedding) and red sandstones of the Río Chico Formation.

Casamayoran fossils from Cañadón Vaca are registered on two measured sections (fig. 8). The lowest fossils in place are about 5 m above the Río Chico contact on section II; three additional fossil levels on section II are at about 12, 18, and 86 m, respectively, above the Río Chico contact. The lowest three of these horizons (sites 3, 4, 5) are highly productive; the small assemblage from site 6 is of great interest because it includes species otherwise unknown from Cañadón Vaca. Two fossil horizons are recorded on section I. Assemblage 1, probably a lateral equivalent to site 4 on section II, produced numerous isolated teeth; assemblage 2, about 41 m higher, includes but a few specimens. The known Casamayoran of Cañadón Vaca thus occupies some 81 m of section, with most specimens deriving from 5 to 19 m above the Río Chico contact.

The known fauna from Cañadón Vaca is given in table 5. Some 30 species of fossil mammals are included; with the exception of site 6, the individual assemblages are highly similar in composition. Assemblage 1 includes nine species not known from elsewhere but it also has the most species, and this difference probably reflects the fact that it is better sampled than the others.

Excluding site 6, the fauna of Cañadón Vaca is strikingly dissimilar to that of the Gran Barranca (tables 1, 2, 5). Of a total of 41[6] identified species collected at known horizons from either locality by the Scarritt Expeditions, only three or four are common to both. The shared species include *Polydolops thomasi, Isotemnus primitivus,* and (with some doubt) *Henricosbornia lophodonta* and *Anisolambda fissidens. Henricosbornia lophodonta,* abundant at Cañadón Vaca, is known

[6] Including the Ameghino Collection, which includes a number of specimens of uncertain exact provenience from the Gran Barranca, the total is about 60.

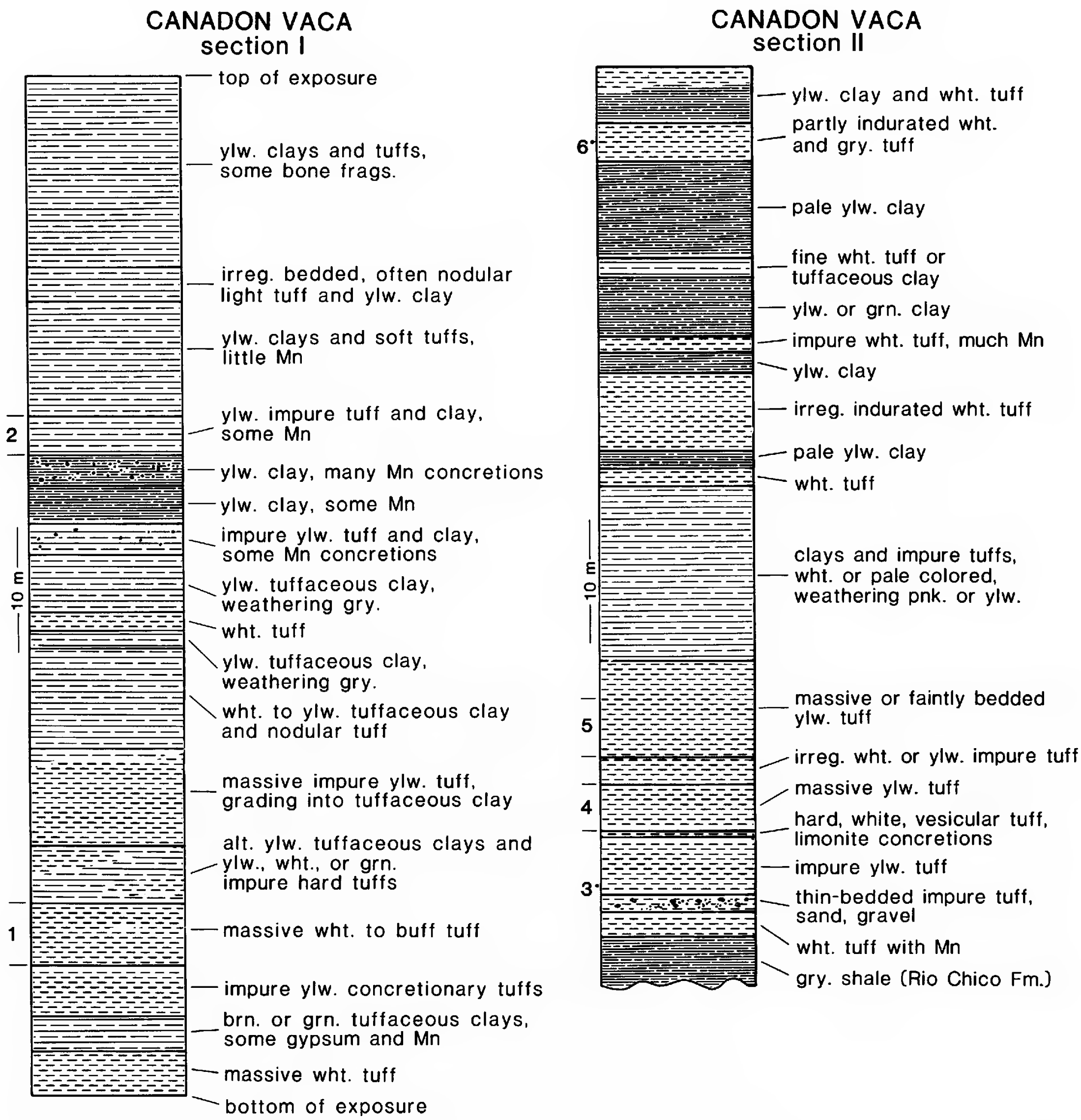

FIG. 8. Measured sections I and II at Cañadón Vaca, west of the Río Chico (see fig. 1), redrawn after fieldnotes of G. G. Simpson. Section I was measured on the southern rim of Pampa Pelada in the upper part of Cañadón Vaca; section II was taken about 5 km east of section I. Numbers at left indicate Casamayoran fossil sites or horizons listed in table 2.

by a single M_2 (AMNH 28726) from the marker horizon at the Gran Barranca. This tooth is somewhat larger than those of the Cañadón Vaca sample. The presence of *Anisolambda fissidens* at both localities depends on hypothetical synonymies which I have presented elsewhere (Cifelli, 1983). Simpson (1948, p. 212) referred two Cañadón Vaca specimens to *Homalostylops parvus* (a species modestly abundant in the upper horizons at the Gran Barranca). These specimens present characters somewhat more primitive than those of the Gran Barranca sample and probably, but not surely, represent a separate yet closely allied species.

Fallaw (1979) has shown that the least

TABLE 5
Composition of Cañadón Vaca Faunules[a]

	1	2	3	4	5	6
Polydolops thomasi	X	X	–	–	–	–
P. borcurhor	X	–	–	–	–	–
Prostegotherium sp. indet.	X	–	–	–	–	–
Didolodus minor	X	–	–	–	–	–
Asmithwoodwardia subtrigona	X	–	–	–	–	–
Victorlemoinea sp. indet.	X	–	–	–	–	–
Anisolambda fissidens	X	–	–	–	–	–
A. amel	X	–	–	–	–	–
Henricosbornia lophodonta	X	–	X	X	–	–
Othnielmarshia lacunifera	X	–	X	–	–	–
Peripantostylops minutus	X	–	–	–	–	–
Notostylops murinus	–	–	–	–	–	X
N. pendens	X	–	X	X	X	–
N. appressus	–	–	–	–	X	–
N. sp. indet.	–	X	–	–	–	–
Homalostylops sp. nov.?	X	–	–	–	–	–
Maxschlosseria consumata	X	–	–	–	–	–
M. minuta	–	–	X	–	–	–
Ultrapithecus cf. *rutilans*	–	–	–	–	–	X
Acropithecus rigidus	X	–	?X	X	–	–
Notopithecus adapinus	–	–	–	–	–	X
Eohyrax praerusticus	–	–	–	–	–	X
Pleurostylodon similis	X	–	X	X	X	–
Isotemnus primitivus	?X	–	X	–	–	–
Thomashuxleya externa	X	–	X	X	X	–
Trignostylops wortmani	?X	–	–	?X	?X	–
Albertogaudrya sp. indet.	–	–	–	–	X	–

[a] Numbers refer to sites or levels in measured sections of figure 7. Data from the collections of the Scarritt Patagonian Expeditions only; occurrence not known by precise stratigraphic horizon ignored. See table 1 for author and date of species.

biased[7] binary coefficient of faunal similarity is that proposed by Simpson (1960); this may be calculated as follows:

$$\frac{C}{N} \times 100,$$

where C is the number of taxa common to both faunas and N is the total number of taxa in the less diverse of the two faunas. Indices of taxonomic resemblance for genera and species from Cañadón Vaca and the Gran Barranca, based on the data of table 1, are 61 and 19, respectively. These figures are comparable to those of some successive land mammal ages; by comparison, a similarly computed index for Gidley and Scarritt quarries, Montana (Torrejonian and Tiffanian North American land mammal ages, respectively) yielded a species value of 38 (Simpson, 1960, p. 310; see discussion below). Assemblage 6, the stratigraphically highest of the Cañadón Vaca sample, is of special interest in this regard because the included taxa (*Notostylops ?murinus, Eohyrax praerusticus, Notopithecus adapinus,* and *Ultrapithecus* cf. *rutilans*) are typical of the Gran Barranca and are otherwise unknown from Cañadón Vaca.

The faunal dissimilarity between these two localities is reflected in a comparison of the relative representation of ungulate families (fig. 9). The Cañadón Vaca fauna is domi-

[7] Raup and Crick (1979) have shown that this coefficient is biased and have developed a probabilistic approach to assessing faunal similarity, using Monte Carlo computer simulations. Further, more detailed analysis of the present data is clearly warranted and will be presented elsewhere.

nated by archaic families (Henricosborniidae, Isotemnidae); the Gran Barranca by more advanced forms (Oldfieldthomasiidae, Interatheriidae). The relative primitiveness of the Cañadón Vaca fauna is reflected also in comparison of sister taxa (closely related species or genus pairs) of the two localities. *Homalostylops* sp. from Cañadón Vaca differs from *H. parvus,* the Gran Barranca species, in being smaller; the cheek teeth are lower crowned, and the median lower molar trigonid cusp is more salient. *Notostylops murinus,* from the Gran Barranca, is advanced with respect to the Cañadón Vaca species (*N. pendens, N. appressus*) in that the upper premolar series is enlarged, with an internal groove on P^{3-4} (Simpson, 1948, pp. 191–201). *Maxschlosseria,* an archaic oldfieldthomasiid (see Bond, 1981) represented at Cañadón Vaca by *M. consumata,* differs from its close relative *Ultrapithecus* (represented at Colhué Huapí by *U. rutilans*) in having lower crowned cheek teeth and relatively smaller posterior upper premolars, with a lesser development of the postcingulum. *Archaeopithecus,* known from the Gran Barranca but not represented in the AMNH collections, is more derived than *Acropithecus* (from Cañadón Vaca) in having more transverse upper premolars (particularly P^{1-2}) and in the reduction of ectoloph folds on the upper cheek teeth (Simpson, 1967b, p. 63). The character polarities of other sister taxa of the two localities are not yet well understood.

It seems unlikely that these faunal differences are ecological in nature. Considered as wholes, each fauna extends through a relatively great stratigraphic section, implying sampling over a long span of time and, in the case of the Gran Barranca at least, the fossils derive from geographically widely distributed places. The two districts are rather close geographically, and there is no geologic evidence to suggest the presence of different climatic regimes or zoogeographic barriers between them. That the faunal differences between Cañadón Vaca and the Gran Barranca are temporal and not ecological is further suggested by lithostratigraphic, biostratigraphic, and paleontologic evidence:

1. The levels of fossil concentration at Cañadón Vaca lie near the base of the "Sarmiento group," beginning several meters above the contact with the Río Chico Formation. No measured section at the Gran Barranca includes this contact; however, the stratigraphically lowest fossil mammals from south of Lago Colhué Huapí probably derive from at least 40 m above the Río Chico contact.
2. The uppermost assemblage (site 6) from Cañadón Vaca, which is considerably higher than the other sites from that locality, shares all its identifiable taxa with the Gran Barranca and none with Cañadón Vaca sites 1–5.
3. The fauna of Cañadón Vaca is more similar to that of the Río Chico Formation than is that of the Gran Barranca (table 6). The archaic nature of the Cañadón Vaca fauna is also reflected in the relative rep-

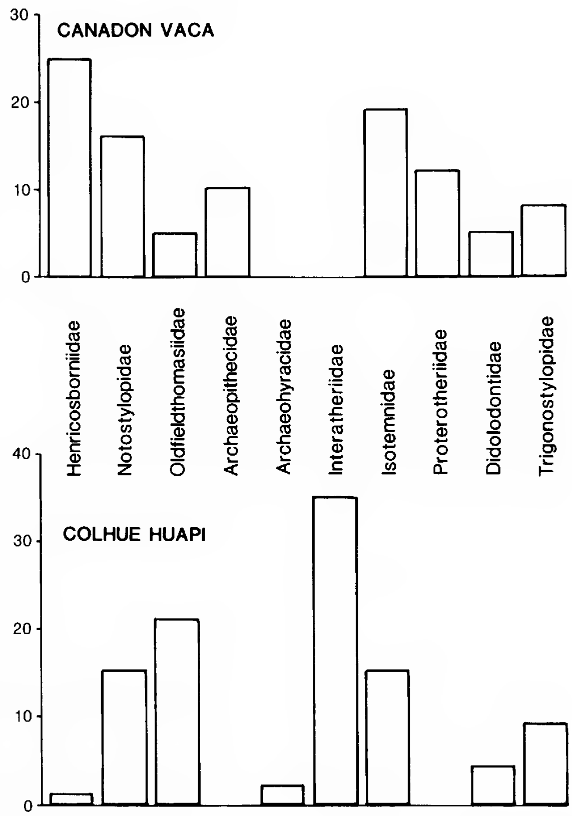

FIG. 9. Comparison of the relative representation of ungulate families between the combined faunas of the Gran Barranca and Cañadón Vaca. Numbers at left refer to total of specimens referable to a given family.

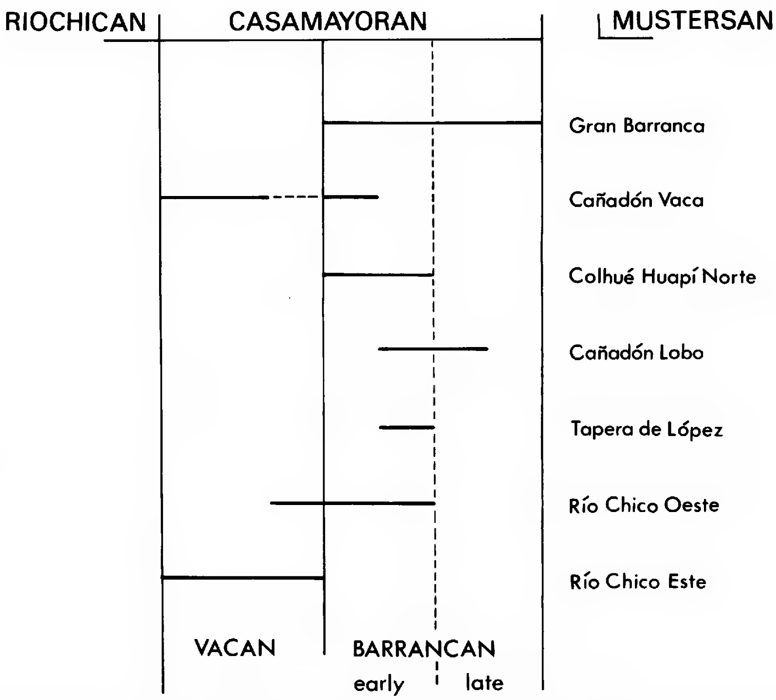

FIG. 10. Hypothesized relative age relationships of the better represented Casamayoran local faunas of Patagonia, using the distributions at the Gran Barranca and Cañadón Vaca as standards for comparison. See text for discussion.

resentation of ungulate families and in the fact that it includes the more primitive members of sister taxa, where they can be identified.

Other Patagonian Localities

It is of interest to consider the compositions of other Casamayoran local faunas in the context of the sequences discussed above, although they are (for the most part) not well represented or understood stratigraphically. Of those listed in table 1, only five additional localities have yielded assemblages including five or more identified mammal taxa. Four of the five (Tapera de López, Río Chico este, Río Chico oeste, Colhué Huapí norte) are regional designations and are not known to be true faunal assemblages; even the exact location of some of the Ameghino localities is unclear (see Simpson, 1948, 1967a; Marshall et al., 1983).

Indices of faunal similarity for these localities and for the Riochican, calculated as before, are given in table 6, and an hypothesis of their relative age relationships is shown in figure 10. The values for these indices corroborate the distinction of the Gran Barranca and Cañadón Vaca assemblages because they show a negative correlation of similarity to the two faunas. The faunas from Colhué Huapí norte, Cañadón Lobo, and Tapera de López are highly similar to that of the Gran Barranca. The exact provenience of the specimens from Colhué Huapí norte (all are in the Ameghino Collection, currently housed in the Museo Argentino de Ciencas Naturales, Buenos Aires) is uncertain. However, the presence of species found in the lower horizons at the Gran Barranca (*Notopithecus adapinus, Trigonostylops wortmani, Pleurostylodon modicus, Thomashuxleya rostrata*) and the absence of species such as *Homalostylops parvus, Ultrapithecus rutilans,* and *Antepithecus brachystephanus* suggest correlation with the lower Gran Barranca assemblage.

Cañadón Lobo (=Cañadón Tournouër), the

TABLE 6
Simpson's Coefficient of Faunal Similarity for Casamayoran Local Faunas and the Riochican

	Gran Barranca	Cañadón Vaca	Colhué Huapí norte	Río Chico oeste	Río Chico este	Cañadón Lobo	Tapera de López
Gran Barranca							
Cañadón Vaca	19						
Colhué Huapí norte	88	0					
Río Chico oeste	35	18	25				
Río Chico este	14	57	0	14			
Cañadón Lobo	80	0	20	20	20		
Tapera de López	86	29	14	29	0	0	
Riochican	29	47	13	21	40	0	29

type Casamayoran (Simpson, 1933), is sparsely fossiliferous and has yielded a small but important fauna. Carlos Ameghino apparently collected only one (unidentifiable) specimen here (Simpson, 1967a, p. 68); the Scarritt Expeditions recovered a single identifiable specimen (*Caroloameghinia mater*; Simpson, 1948, p. 38) at Cañadón Lobo. The main collection from this locality is that made by André Tournouër in 1903, described by Gaudry (1906) and by Simpson (1964, 1967b). The "Sarmiento group" is represented here by about 69 m of alternating tuffs and claystones, occasionally with manganese nodules, overlying an unknown thickness of opalized tuffs and clays. The Monte León Formation overlies the "Sarmiento group" at Cañadón Lobo. Simpson discovered unidentifiable mammal bones approximately 25 m above the silicified tuffs and clays on the north side of Cañadón Lobo and about 21 m above the same on the south side of the cañadón. (The single identifiable specimen collected by the Scarritt Expeditions was found on the surface and its exact provenience is uncertain.) Of the modest fauna, *Trigonostylops wortmani, Oldfieldthomasia* sp., *Utaetus buccatus,* and *Antepithecus brachystephanus* are Gran Barranca forms; the presence of these taxa best known from the marker horizon, but commonly found above and below it, indicates probable correlation with the marker bed.

Casamayoran mammals were collected near the Tapera de López, Chubut, by the second Scarritt Patagonian Expedition (1933–1934) and were described by Simpson (1948, 1967b). Work in progress indicates that these mammals came from several districts and that, because the geology of the region is not yet well understood and because much of the region is covered with vegetation, the stratigraphic relationships of these areas cannot now be determined. Two species (*Isotemnus ?primitivus* and *Polydolops thomasi*) are shared with both Cañadón Vaca and the Gran Barranca; several other species are shared only with the latter locality but, with the exception of *Notopithecus adapinus,* they are not very diagnostic for purposes of chronologic correlation because of their rareness. Marsupial specimens were recovered in unusual abundance from the Tapera de López.

The correlation of Ameghino's localities along the Río Chico is less clear. Their precise location is not known, and probably one, or both, represents an area rather than a circumscribed fossil locality. Many species from west of the Río Chico are represented by single specimens, holotypes, and are unknown elsewhere; they are thus of no help in relative age determination. The presence of *Oldfieldthomasia debilitata, Trigonostylops wortmani, Anisotemnus distentus,* and *Notopithecus adapinus* suggests an age roughly equivalent to that of the lower part of the Gran Barranca section; nonetheless, the large isotemnids *Pleurostylodon similis* and *Thomashuxleya externa* are common to Cañadón Vaca but not to the Gran Barranca. Perhaps the Río Chico oeste locality represents an assemblage from different stratigraphic horizons, or perhaps it represents a local fauna intermediate in age between well known Cañadón Vaca and Gran Barranca assemblages.

The fauna from east of the Río Chico strongly resembles that of Cañadón Vaca in that it includes *Maxschlosseria* spp., *Notostylops pendens, Edvardotrouessartia sola, Acropithecus rigidus, Thomashuxleya externa,* and especially the henricosborniids *Henricosbornia lophodonta, Othnielmarshia lacunifera,* and *Peripantostylops minutus.* Contradictions to correlation with Cañadón Vaca

TABLE 7
Generic List of Riochican Mammals from Patagonia

Seumadia	*Othnielmarshia*
Polydolops	*Peripantostylops*
Gashternia	*Kibenikhoria*
Ernestokokenia	*Maxschlosseria*
Victorlemoinea	*Seudenius*
Wainka	*Isotemnus*
Anisolambda	*Shecenia*
Henricosbornia	*Carodnia*

TABLE 8
Simpson's Coefficient of Faunal Similarity (Genera) for North American Early Tertiary Land Mammal Ages[a]

Ages	Index
Puercan-Torrejonian	30
Torrejonian-Tiffanian	44
Tiffanian-Clarkforkian	53
Clarkforkian-Wasatchian	63

[a] Data from Savage and Russell, 1983. Highly dubious occurrences were ignored. Wasatchian includes Gray Bull, Lysite, and Lost Cabin faunas; all are composites.

are the rare species *Paginula parca* (otherwise recorded from Cerro Negro and the Cañadón Lobo local fauna, of probable Gran Barranca age), and *Anisotemnus distentus,* a species shared with the Gran Barranca fauna.

DISCUSSION

Casamayoran Land Mammal Age Boundaries

The problem of defining land mammal ages in South America is particularly acute because, except for the appearance of rodents and primates in the ?late Eocene and the great interAmerican interchange (which began at the close of the Miocene), no immigrants are available for use as "datum planes." It is to be expected that as transitional faunas become known, the distinctions between land mammal ages will become less evident; many of the classic faunal distinctions in South America's Tertiary record are based on observed hiatuses in the record.

A generic list of Riochican mammals from Patagonia is given in table 7 (a composite species list is given by Savage and Russell, 1983, p. 46). *Transpithecus* and *Notopithecus,* typical Casamayoran genera, were included in the Riochican faunal list of Simpson (1967b, p. 249); I here more conservatively refer them to Notopithecinae, indet.[8] Simpson (1935a) divided the then known Riochican into three zones, named after taxa typical of each: *Ernestokokenia chaishoer,* the youngest, including mammals from the Bajo de la Palangana upper sandstone; *Kibenikhoria,* intermediate in age, including the Cañadón Hondo sandstone fauna; and *Carodnia,* the oldest, including lower Bajo de la Palangana fossils and those from Cerro Redondo. Simpson (1935a) noted that, with the exception of the few known taxa from the *Carodnia* zone, the fauna considered as a whole is similar to that of the Casamayoran and that distinction between the faunas is somewhat arbitrary with respect to intermediate assemblages. Of the 17 genera recognized here from the Riochican of Patagonia, nine are also known from the Casamayoran. The index of faunal similarity between the two land mammal ages, 53, is comparable to indices for the Paleocene and early Eocene land mammal ages of North America (table 8). Of Casamayoran local faunas, Cañadón Vaca and Río Chico este are most similar to the Riochican (see table 6).

With the possible exception of *Periphragnis* and several other (highly dubious) occurrences (see Simpson, 1948, 1967b), no genera are known from both the Mustersan and Casamayoran. Pascual (1965) referred a local fauna that he collected at Paso de los Indios, Provincia del Chubut, to the Casamayoran, but noted that it is not typical and in some respects is more similar to Mustersan assemblages. He did not supply a faunal list, but the basis for this assessment seems to be: (1) the relatively advanced morphology of the isotemnid notoungulates and of *Oxybunotherium praecursor,* and (2) the absence of *No-*

[8] These and other Casamayoran taxa (both genera and species) are recorded in the Riochican by Pascual, as noted above. Precise boundary circumscription of the Casamayoran must await detailed study of relevant Mustersan and Riochican assemblages, especially that of the Bajo de la Palangana upper sandstone.

tostylops and of henricosborniid notoungulates, and the rarity of *Homalostylops*. *Oxybunotherium*, based on lower molars, is a probable synonym of *Proectocion*, based on upper cheek teeth (Cifelli, 1983). The exact proveniences of the holotypes of the dubiously distinct *P. argentinus* and *P. precisus* are not known, but they were collected in the Casamayoran beds south of Lago Colhué Huapí (Simpson, 1948, pp. 108–109); a specimen surely conspecific with the holotype of "*Oxybunotherium praecursor*," AMNH 28769, was collected by the first Scarritt Patagonian Expedition in Valle Hermoso (southeast of the main barranca). The associated fauna includes *Notopithecus adapinus* and *Trigonostylops ?wortmani*; correlation with the lower portion of the Gran Barranca section therefore seems most probable. The absence of henricosborniid notoungulates at Paso de los Indios is thus unsurprising; the significance of other absences (such as *Notostylops*) cannot be evaluated without a complete faunal list and relative abundance data.

Nearly all of the genera and species hitherto referred to the Casamayoran are therefore characteristic of it, but the present study indicates that many of them are rare or are confined to given stratigraphic intervals within it; except for taxonomic revisions incorporated here, these results are in agreement with the faunal list given by Pascual and Odreman Rivas (1971). *Notostylops*, for which the fauna was originally named, is restricted to and spans the entire Casamayoran recognized here. Judged by their presence in the Gran Barranca, Cañadón Vaca, and other Patagonian local faunas, it seems likely that *Polydolops thomasi, Homalostylops, Eohyrax, Isotemnus primitivus, Thomashuxleya*, and *Trigonostylops* have nearly the same range. They may be taken as index taxa for the Casamayoran Land Mammal Age, and their first appearance distinguishes the Casamayoran from the Riochican.

SUBDIVISIONS OF THE CASAMAYORAN

The foregoing analysis indicates the faunas of the Gran Barranca and Cañadón Vaca to be markedly different. Because this difference results from the greater antiquity of Cañadón Vaca and because the difference is recognizable in other local faunas of Casamayoran age in Patagonia, two distinct Casamayoran subages may be recognized. For these I propose the names Barrancan and Vacan. The index of generic similarity between the two subages, 61, is approximately equal to that for the Clarkforkian and Wasatchian land mammal ages of North America (63; see table 8). Riochican mammals are now known from the Río Chico Formation at Cañadón Vaca (M. F. Soria, personal commun.) and, because a Barrancan assemblage is also known from that locality (site 6, section II; fig. 8), the Vacan is thus known to be bounded by preceding and succeeding faunas in stratigraphic superposition. Vacan mammals are not yet known from the Gran Barranca, but the Barrancan fauna is there bounded above by the Mustersan. As identified by the first appearance of abundant and characteristic taxa, these subages may be defined as follows:

Vacan	Barrancan
Anisolambda amel	*Utaetus*
Othnielmarshia lacunifera	*Didolodus multicuspis*
Peripantostylops minutus	*Oldfieldthomasia debilitata*
Notostylops pendens	*Homalostylops parvus*
Notostylops appressus	*Oldfieldthomasia debilitata*
Maxschlosseria consumata	*Ultrapithecus*
Acropithecus	*Acoelodus*
Thomashuxleya externa	*Paginula*
	Notopithecus
	Eohyrax isotemnoides
	Thomashuxleya rostrata
	Antepithecus brachystephanus

Superpositional (and therefore probably age related) faunal change is evident within the Barrancan. Some of the observed distribution patterns may reflect sampling inadequacies; nonetheless, an "early" and a "late" Barrancan may be informally distinguished by the presence or absence[9] of characteristic and abundant species:

[9] All of these species occur together in the marker horizon. The subspecies *Notopithecus adapinus reduncus* is totally restricted to the early Barrancan.

TABLE 9
Ameghino's Subdivision of the Casamayoran

Ameghino, 1902	Simpson, 1967a[a]
Notostylops superior	
Notopithecidae	*Utaetus lenis*[b]
Archaeopithecidae	*Machlydotherium sparsum*[b]
Henricosbornidae [sic]	*Meteutatus percarinatus*[b]
Carolozittelia	*Utaetus buccatus*
Albertogaudrya	*U. deustus*
Thomashuxleya	*Prostegotherium astrifer*
Didolodus	*P. notostylopianum*
Euprotogonia [*Ernestokokenia*][c]	*Pseudostegotherium chubutanum*
Prohyracotherium [*Henricosbornia*]	*Paulogervaisia mamma*
Lophiodonticulus[b]	*Paulogervaisia porca*
Eochalicotherium [*Isotemnus*][c]	*Paulogervaisia inusta*
Isotemnus	"*Acoelodus*" *priclivus*
Selenoconus [*Henricosbornia*][c]	*Maxschlosseria minima*
Nephacodus [*Didolodus*][c]	*Eohyrax rusticus*
Paulogervaisia	*Pleurostylodon modicus*
Trigonostylops	*Isotemnus colhuehuapensis*[b]
Notostylops	*Anisotemnus distentus*
Acelodus [sic]	*Pleurostylodon crassiramus*[b]
Oldfieldthomasia	*Albertogaudrya unica*
Miolania argentina[d]	
Dinosaurs	
Notostylops inferior	
Caroloameghinia	*Utaetus buccatus*
Maxschlosseria	*Maxschlosseria praeterita*
Ernestokokenia	*Notopithecus adapinus*
Amilnedwarsia [sic]	
Rutimeyeria	
Polydolops	
Ideodelphis[b]	
Argyrolestes peralestinus	
Nemolestes spalacotherinus	
Dinosaurs	

[a] After revisions by Simpson, not the name originally published.
[b] Status dubious or uncertain.
[c] Names in brackets follow revisions by Simpson, 1948, 1967b.
[d] Not a mammal, but a horned turtle.

Early Barrancan	Late Barrancan
Notopithecus adapinus	*Homalostylops parvus*
Oldfieldthomasia debilitata	*Ultrapithecus rutilans*
Pleurostylodon modicus	*Antepithecus brachystephanus*
Notostylops murinus	

Most of the other well known Casamayoran localities of Patagonia are comparable to the Gran Barranca in content; Ameghino's localities east and west of the Río Chico include (in different proportions) mammals of both Barrancan and Vacan age and therefore may partly occlude the gap between the type faunas (see fig. 10).

Ameghino (1902) distinguished two subdivisions of what is now known as the Casamayoran fauna, a "Notostilopense superior" and a "Notostilopense inferior," and later (1903) added a "basal" part (table 9). Ameghino's lists for the superior and inferior *Notostylops* faunas are compared to designations he left with his collections or transmitted orally to Simpson by Carlos Ameghi-

no (Simpson, 1967a; see discussion of the "basal" *Notostylops* therein). The basis for these subdivisions is not now evident and may have been in part hypothetical. In several instances (such as the assignment of *Oldfieldthomasia* to the "Notostilopense superior" and of *Maxschlosseria* to the "Notostilopense inferior") Ameghino's referrals are in accord with those of the present study, but the faunal lists are otherwise so contradictory that his zonation cannot be said to have an adequate basis.

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